## Some Correlations of Leaves

By Daniel Trembly MacDougal

As a result of a long series of experimental tests made in the New York Botanical Garden, Mr. Charles Zeleny has found that the excision of one of the leaflets of such plants as *Trifolium pratense* (clover), *Parthenocissus quinquefolia* (Virginia creeper) and *Lupinus albus* (white lupine) resulted in alterations in the positions of the remaining leaflets, alterations in the intervals between the remaining members and divergences from the normal size.

Our knowledge of correlations at the present time would lead to the expectation that organs, the activity of which was complementary or dependent upon a removed organ would show a decreased or diminished development. On the other hand the small amount of evidence available would have led to the generalization that the loss of an organ or a part of an organ would stimulate the development of the remainder of the organ, or of the tissues carrying on the same function, in a supposed effort to bring the total functional performance up to the normal average. Mr. Zeleny's results, however, demonstrate unequivocally that the excision of a leaflet in the above species is followed by a diminished development on the part of the remainder, which results in the accomplishment of a superficial extension, as represented by the length of the members, about seven per cent. less than the normal.* Results fairly in agreement with those of Mr. Zeleny have also been obtained by Nemeč by less exact methods.†

Goebel cites the fact that the stipels of the compound leaves of *Robinia Pseudacacia* (locust) reach an abnormally large size when the leaflets are removed, which is an example of the induced enlargement of a structure in the effort to carry out the functions of lost tissue.‡ He has also found that the destruction of the vegetative points on such leaves as those of *Bryophyllum* is

* Read before the Botanical Society of America, Pittsburg, July 1, 1902. Now in press in Bull. N. Y. Bot. Garden, vol. 3, no. 9.

† Nemeč, B. Ueber die Folgen einer Symmetriestörung bei zusammengesetzten Blättern. Bull. Internat. Acad. Sci. Bohême. 1902.

‡ Goebel. Organography of Plants, 1 : 210. 1900.

followed by the formation of new ones at places nearer the base of the leaf-blades.* It is evident therefore that the epipodium, or laminar portion of the leaf, is capable of the most diverse correlative reactions according to the structure, and adaptive, or secondary functions it has acquired.

The lack of uniformity in the facts at hand suggested that a repetition of some of the experimental tests with additional species might yield results of value. To this end the author made a series of observations upon the effect of the removal of the epipodium and mesopodium of the leaves of one species upon the stip-

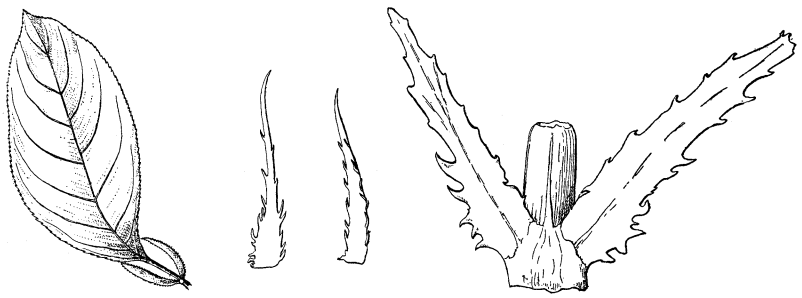


FIG. 1. *Prunus serotina*. A, normal leaf, × ½. B, normal stipules, × 3. C, leaf-base with enlarged stipules; the stump of the excised petiole is shown, × 3.

ules of the hypopodium and upon the vegetative points of the stems from which the leaves arose. Additional observations were carried out on the influence of the removal of a leaf showing only a distinct mesopodium (petiole) and epipodium (lamina) upon the vegetative points of the stem and upon the development and differentiation of the tissues of the stem.

A small specimen of *Prunus serotina* growing near the propagating houses of the New York Botanical Garden was selected for the first test. All of the young unfolding leaves, except those of one basal branch, were dissected by the excision of the petiole near the stipules on April 24, 1903. None of the leaves had unfolded on the above date. The plant was visited daily and the successive leaves removed in the same manner leaving the stipules intact. A number of the other small trees of the same species

* Goebel. Regeneration in Plants. Bull. Torrey Club, 30 : 197–205. 1903.

growing near by were also available for comparison. The earlier part of the season was one of extreme drought. During the period of fifty-two days between April 16, a week before the beginning of the test, a total precipitation of only 1 cm. was recorded. It was noted that the scales and stipules were of longer duration and presented the appearance of increased superficial extension upon the delaminated branches within a fortnight after beginning the tests. The development of leaves and buds appeared to have almost ceased and an anatomical examination was made June 3–10 with the following results:

The greatest length made by branches which had been defoliated from the beginning was 18 cm., while a length of 25 and 30 cm. was found in normal branches; 18–20 leaves had been formed on defoliated branches and but 14 or 15 on normal ones. The basal internodes of the twigs showed but little difference in length in the two instances, being as much as 2 cm., although less in some cases. The internodes formed later in the season on the normal twigs attained a length of as much as 3.5 cm. in some instances, while those of the defoliated twigs varied from 1.5 cm. to one third that length. Consequently the defoliated twigs were closely crowded at the terminal part with scales and stipules. This crowding effect was accentuated by the fact that one or two small leaves were thrust out of the axillary buds, although no general activity of the bud was exhibited. In contrast with the behavior of *Acer*, it could not be made out that any extra number of lateral buds on the older parts of the branches below had been induced to awaken.

The correlative alterations in the stipules were very marked and consisted in changes in form, size, position, structure and period of endurance. Normal stipules of the cherry are thin-membranaceous, and generally of a reddish tinge containing almost no chlorophyl. These stipules are usually short-lived and fall off in such manner that on the above date they could be found only on two or three leaves on the terminal portions of twigs. The stipules on twigs on which the leaves had been dissected were both broader and longer, offering a superficial expansion of about five times the normal (see *f.* 1). The maximum measurements were but little greater than those of normal stipules formed earlier

on the first internode, but their length, width and thickness was such as to give the exaggerated extension noted above when compared to correspondent structures on normal branches. Furthermore, three pairs of stipules were present on normal twigs and ten

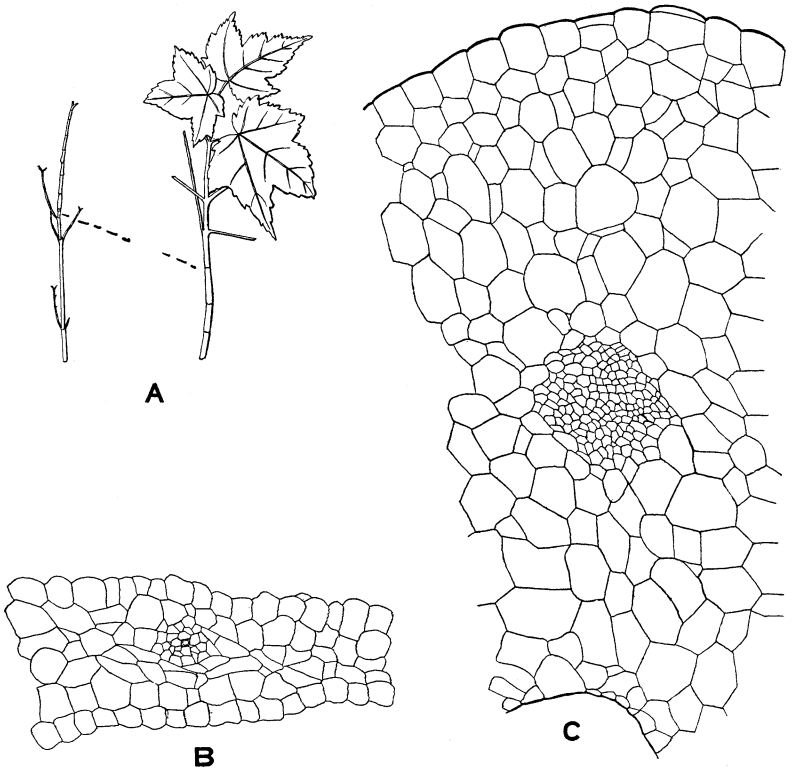


FIG. 2. A, *Acer;* normal and defoliated branches. The dotted line shows the bases of new growth. B, *Prunus;* transverse section of normal stipule. C, *Prunus;* transverse section of stipule of delaminated leaf. B and C are drawn to same scale.

pairs on those which had been defoliated. It is thus to be seen that twigs which had been deprived of the laminar portions of the leaves made such development and retention of the stipules that they were able to expose about fifteen or sixteen times as much stipular surface as normal correspondent branches.

The increase of the stipular surface consequent upon the removal of the laminae is not unknown, and Goebel notes that simi-

lar reactions are shown by the elder (*Sambucus nigra*).* He also found that the stipules of *Vicia Faba* were increased in superficial extension two to six times beyond the normal by the excision of the laminae in an early stage of development, and a similar exaggeration in the stipules of *Lathyrus Aphaca* resulted from the cessation of elongation or extension of the shoots. This correlation is not present in all plants, however, and not even in all Papilionaceae, since it was seen that the excision of the laminae of *Phaseolus multiflorus* had but little effect upon the size and structure of the laminae.†

The excision of the leaves of *Aristolochia*, in the course of the present experiments, did not cause any notable increase in size of the stipules as seen by general inspection, although no examination of the internal structure was made.

Kronfeld made a series of experimental tests of this matter in 1886, and found that the stipules of *Pyrethrum Indicum*, *Rosa semperflorens*, *Rubus fruticosus*, *R. Idaeus*, *Sida Napaea*, *Trifolium filiforme* and *Urtica urens* were not sensibly increased in size by the destruction of the laminae. The destruction of the laminae of *Pyrus Malus* was followed by an increase of the superficial expansion of the stipules amounting to a hundred per cent. The excision of the laminae of *Pisum sativum* was followed by an increase of the size of the stipules amounting to from fifty to one hundred per cent., while the excision of the stipules alone seemed to have the effect of causing earlier flower-formation. ‡

Stomata were found on both normal and abnormal stipules in *Prunus* in my own experiments. No examination of the number of stomata on the adjoining surfaces of the stem were made, but Braun has found that defoliation causes the formation of an increased number of these organs. § The enlargement of the stimulated stipules of *Prunus* had apparently not been accompanied by a multiplication of the epidermal cells, since these elements were both larger and wider in surface view than the normal.

* Goebel. Organography of Plants, 1 : 210. 1900.

† Goebel. (Beiträge zur Morphologie und Physiologie des Blattes.) Bot. Zeitung, 38 : 836–837. 1880.

‡ Kronfeld, M. Ueber die "Correlation des Wachstums." Bot. Zeitung, 44 : 846–849. 1886.

§ Braun, K. Ueber Veränderungen im Gewebe entlaubter Stengel und Zweige. (Inaug. Diss.) Erlangen. 1899.

The enlarged stipules exhibited a thickness four or five times as great as the normal, chiefly due to increase in tissues and differentiations toward the structure of a typical lamina. A median layer of loosely arranged parenchymatous tissue contained much chlorophyl which was almost wholly lacking from the normal organ. This mesophyllary tissue also exhibited numerous intercellular spaces, and was altogether well adapted to carrying on photosynthetic and transpiratory functions.

The entire stipule, which is usually closely appressed to the petiole, was held at a more widely divergent angle than the normal. These adaptations have greater significance when it is understood that the total amount of stipular surface presented by a delaminated branch would amount to about fifteen or sixteen times as much as the normal. This comparatively normal increase, however, does not result in developing a foliar surface of more than one or two per cent. of that of the normal leafy branch.

Sections of the sixth internode from the base of the twigs formed in 1903 were examined in order to ascertain the effect of deprivation of the laminar structures and their partial replacement by the stipules. It has already been pointed out that the branches which had been delaminated had developed more internodes, the total lengths of which were less than of twigs normally grown, and had the appearance of being slightly thicker, but no measurements were made which might form the basis of an exact comparison. The epidermal tissues of the treated branch had greater radial and tangential diameters, and the underlying collenchymatous layers were but slightly thickened. The medio-cortex contained much more chlorophyl than the normal. The bast fibers were not so heavily thickened as in the normal, and the walls of all the internal tissues exhibited a slight yellowish tinge. The cambium showed a greater number of layers than the normal. The xylem was irregularly developed and seemed to have attained a less advanced stage of differentiation in its various elements than in the normal. The tangential development was notably deficient and the separate bundles were separated by wide rays of pith.

On June 15 the delaminated branches had assumed the appearance of a resting stage. The formation of leaves had ceased, and nearly all of the stipules had fallen off. The buds in the axils of

the newly formed branches were enclosed and in the winter condition. My absence from the Garden during July prevented observations being taken during a period of four weeks, but an examination of the plants on July 30 showed that all of the newly formed delaminated branches of this season had perished and that buds on the older branches had awakened and extended to a length something less than the normal growth of the earlier part of the season.

The increase in the amount of chlorophyl in the cortex may be considered as a further effort to meet the losses ensuing from the lack of the laminar portions of leaves. The non-development of the phellogen and the imperfect construction of the bast fibers and fibrovascular bundles may be ascribed in part to a lack of formative material and in part to the absence of the stimulation ensuing from the decreased transpiration stream and the material usually formed in the laminae. In addition, the mechanical strains and stresses exerted by the foliar organs undoubtedly exert some stimulative effect on the rigidity and pliability of the stems by the induction of the development of various mechanical elements. The absence of stimuli of this character would account in part for the imperfect development of the stems.

The tests with *Acer* were much more restricted. The petioles were excised near the base and the effect upon the activity of the vegetative points noted. Only a single basal branch of a small tree was treated in this manner, and comparisons were made with corresponding portions of similar branches arising from the same part of the central stem.

The single normal branch taken for comparison developed four internodes which had a diameter about thirty per cent. greater than the internodes of the defoliated branch. The total length of the four newly formed internodes amounted to 78 mm., the longest being the third from the base of the yearly growth, measuring 25 mm. Eight active functional leaves were developed. (One has been cut away in the illustration, *f.* 2, *A.*) The newly-grown part of the defoliated branch measured 48 mm. and comprised seven internodes, the longest of which was the sixth from the base, measuring 8 mm. The excision of the leaves had induced the development of one bud in the axil of the last internode of the previous season. The branchlet thus formed showed two long

internodes, the basal one of which measured 14 mm. Two branchlets were produced at the next node below on the newly-formed portion of the main branch, which showed two and three internodes and were 10 and 15 mm. long respectively. The third internode below produced two branchlets 6 and 12 mm. long and composed of two internodes.

The lateral branchlets of the main branch showed less total growth and also less marked development of the lateral buds correspondent to the general habit of the normal. Activity of the vegetative points on the defoliated and normal branches had practically ceased on June 15, the mutilated branch showing no prolongation of the period. The departures from the normal structure of the stem were fairly similar to those described in *Prunus*. Chlorophyl was quite as profusely developed in the normal as in the treated branch, however, and was found in the medullary rays in great abundance.

The above results are found to agree in the main with those of Boirivant, who practiced defoliation and delamination and noted the effect upon stems and upon petioles of *Faba vulgaris*, *Sarothamnus scoparius*, *Genista tinctoria*, *Lathyrus odoratus*, *Chenopodium album*, *Atriplex nitens*, *Linum usitatissimum*, *Galium Cruciata*, *Asparagus officinalis*, *Robinia Pseudacacia*, *Arachis hypogaea* and *Ailantus glandulosa*.* It is to be noted, however, that the epidermal tissues in my material showed enlargement in the tangential axis, and one or two other minor differences appear. Boirivant's studies included a consideration of the anatomy of the petioles of leaves of which the laminae had been cut away, and in these organs he found an exaggerated production of chlorophyl, modifications of the cortical tissues consisting of added differentiations of palisade tissue, and enlargement of the vessels and more lignification of the tracheids and pith. I am not able to find that he noted the effects of the treatment upon the stipels of *Robinia*, or made observations upon the reaction of the hypopodium especially.

The observations of Braun also extend over the matter of the effect of delamination on stems. His observations included

* Boirivant, A. Recherches sur les organes de remplacement chez les plantes. Ann. Sci. Nat. Bot. VIII. 6: 309–400. 1897.

*Lamium Orvala, Aconitum Stoerkianum, Clematis Vitalba, Syringa vulgaris, Corylus Avellana atropurpurea, Gillenia trifoliata, Prunus Mahaleb, Aesculus Hippocastanum, Ampelopsis hederacea, Aristolochia Sipho, Acer platanoides, Rosa centifolia* and *Phaseolus multiflorus.** In addition to results previously cited, Braun concludes also that the effect of delamination is to increase the photosynthetic capacity of stems, retard the development of internodes and interrupt the formation of woody tissue, all of which is confirmed by my own results. Braun also suggests that the condition of delaminated stems may be regarded as pathological, and that it is directly due to mechanical interferences with the functions involved. The condition of delaminated branches is undoubtedly one of hypoplasia, but a careful consideration of the various features involved leaves but little doubt that the failure to develop is largely due to the absence of the customary stimuli in response to which the several tissues carry on growth and differentiation in a normal manner. The results in question are quite as much a matter of correlation dependent upon stimulative factors, as the variations in position and growth in compound leaves as discovered by Zeleny.

The more important facts observed as a result of cutting away the laminae of the leaves of *Acer* and *Prunus* by severing the petiole near the base may be briefly summarized as follows:

I. The duration of the stipules of *Prunus* is increased, so that ten pairs of these organs are to be found on branches at a time when only two or three pairs are present on a normal branch.

II. The stipular surfaces exposed on delaminated branches of *Prunus* were sixteen times as great as on normal branches.

III. The individual stipules of *Prunus* were of a maximum measurement in length and width on the delaminated branches and were much larger than the stipules present on the corresponding part of normal branches.

IV. The position of the stipules of *Prunus* on delaminated leaves was more divergent than the normal, and approximated that of a typical leaf.

V. The structure of the stipules of *Prunus* was modified in

* Braun, A. Ueber Veränderungen im Gewebe entlaubter Stengel und Zweige. (Inaug. Diss.) Erlangen. 1899.

such manner as vastly to increase their capacity for photosynthesis and transpiration.

VI. The loss of the lamina acts as a stimulus which induces a development and differentiation of spongy parenchymatous and other tissues in the stipule, and the formation of chlorophyl.

VII. The lateral buds of *Acer* on internodes formed during the previous season were awakened by defoliation of the extending apical portion.

VIII. The period of activity of the vegetative point of the terminal portion of a woody branch is not lengthened as a result of defoliation.

IX. The total length of the newly formed portion of the branches defoliated during growth was thirty to sixty per cent. less than that of normal branches occupying the same relative positions on the shoot.

X. The number of internodes developed on defoliated branches was greater than in the normal.

XI. The defoliated internodes were of a diameter not greater, sometimes less than the normal, and had accomplished less perfect differentiation.

XII. Branches compelled to accomplish growth in a defoliated condition generally are found to be in a state of hypoplasia, the undeveloped and imperfectly differentiated condition of the tissues being due to the lack of correlative stimuli.

New York Botanical Garden.